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Effects of artificial warming on stem radial changes in Qinghai spruce saplings in the Qilian Mountains of China

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ABSTRACT

Climate change has been documented in the Qilian Mountains of China, and the response of tree stem growth to environmental factors may be changed, affecting regional estimates of seasonal growth patterns and carbon sequestration. The objective of this study was to provide initial evidence for responses of intra-annual tree stem radial changes of sapling Qinghai spruce (*Picea crassifolia*) to climate warming in the Qilian Mountains. We monitored stem radial changes of Qinghai spruce in an open-top chamber (OTC) and out of chamber (OC) over three growing seasons (2014–2016) using high-resolution point dendrometers. Statistical analysis indicated that the differences in annual average air temperature between OTC and OC were about 1 °C. Our results showed that the onset of the main growth period in OTC was about one week earlier than in OC, and soil temperature played an important role in controlling the onset of growth in sapling Qinghai spruce. However, the timing of radial growth cessation exhibited large variability in different growth conditions. These results indicated that the end of growth may not be related to environmental factors. Daily average air temperature, vapor pressure deficit, relative air humidity, and precipitation were significantly correlated with daily stem radial increment (SRI) and tree water deficit (TWD). Further, soil water content and TWD were also correlated. SRI in OTC was larger than that in OC, while TWD exhibited no significant differences between the two growth conditions. However, cumulative seasonal growth may not be influenced by air temperature alone, but by interacting environmental factors.

1. Introduction

Over the past decades, climate change led to rising temperatures and changes in the timing and magnitude of precipitation with possible cascading effects on tree-available water and changes in phenology, growth, and water relations in forests (IPCC, 2013; Brinkmann et al., 2016; Zeppel et al., 2014). Climate change directly affected above-ground biomass in forests (Chen and Luo, 2015), while climate change-resultant droughts consistently decreased growth and increased mortality rates of trees (Bennett et al., 2015). Daily stem radial changes and the formation of tree-rings were also affected by climate change (Duchesne et al., 2012; Yang et al., 2017).Previous dendroclimatological studies focused on the response of inter-annual tree growth to environmental factors. However, shorter time-scale responses of tree growth to environmental factors are needed to better understand how specific environmental factors influence the formation of tree-rings.

Daily stem radial changes can be continuously monitored without invasive sampling using dendrometers (Devine and Harrington, 2009; Deslauriers et al., 2011), which also include information on stem radial growth and fluctuations in tree water use due to imbalances between transpiration and root water uptake (Steppe et al., 2006; Zweifel et al., 2006). Thus, several authors used dendrometers to study the effects of environmental factors on tree growth and water status (Turcotte et al., 2009; Oberhuber and Gruber, 2010; Drew et al., 2011; Oberhuber et al., 2015a, b; Da Silva Sallo et al., 2017), which reported that temperature was the most important factor limiting the initiation of growth (Deslauriers et al., 2008; Moser et al., 2010; Rossi et al., 2011; Lenz

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Fig. 1. Study site and the open-top chamber for the warming experiment. (The blue box represent control plot and the red box represents the warming-experiment plot) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

et al., 2013) and moisture availability was the major limiting factor of stem growth (Xiao et al., 2014; Jiang et al., 2015).

The Qilian Mountains, on the northeastern border of the Tibetan Plateau, are the most important water source for the arid area of northwestern China, feeding the Shiyanghe, Shulehe, and the Heihe Rivers. The climate of the Qilian Mountains is representative of the transition zone between monsoon and continental climate, and is affected by multiple climate factors. Under global climate change, temperature and heavy rainfall events increased, while the frequency of precipitation decreased in this area (Liu et al., 2005, 2007; Lin et al., 2017).

Forests in the Qilian Mountains play a vital role in water conservation; they prevent the development of desertification and maintain the stability of oasis ecosystems in the middle and lower reaches of the inland river system (Xu et al., 2009b; Chang et al., 2014). The Qinghai spruce (*Picea crassifolia*), commonly found in the Qilian mountains, grows on shaded or semi-shaded slopes at elevations of 2600–3400 m (Zhao et al., 2006), and constitutes one of the most important long-lived evergreen species in this area. Due to its sensitivity to climate change, Qinghai spruce has been widely used in dendroclimatological studies (Liang et al., 2006b; Zhang and Wilmking, 2010; Wang et al., 2016a, b). Most of the studies focused on the response of tree-rings to environmental factors (Gou et al., 2005; Wang et al., 2016a, b) and on the reconstruction of past climate (Liang et al., 2006a; Liu et al., 2007; Chen et al., 2013; Deng et al., 2013). However, the responses of daily stem radial changes to environmental factors, especially in a warming climate, remain unclear (Tian et al., 2017).

Previous research on assessing the impacts of future climate warming on tree growth analyzed differences in tree growth across altitudinal gradients because such gradients allow for 'space-for-time/warming experiments' (Moser et al., 2010; Jochner et al., 2013). A more direct approach in warming experiments is to employ open-top chambers, and several open-top chamber studies addressed the impacts of increased temperature on plant growth, photosynthesis, nitrogen mineralization, and carbon sequestration (Rustad et al., 2001; Hyvonen et al., 2007; Way and Oren, 2010; Wu et al., 2011; Chung et al., 2013). However, most of the warming experiments were conducted in meadows or shrubs lands (Xu et al., 2009a; Zhang et al., 2015), and it was poor about the study of arbors in China.

To better understand the effects of climate warming on stem radial changes in Qinghai spruce, we established an open-top chamber (OTC) for warming experiments. Growth of Qinghai spruce saplings was monitored in the OTC and out of the chamber (OC) using high-resolution automatic point dendrometer over three growing seasons; environmental factors were monitored synchronously. The main objectives of this study were to provide initial evidence of (1) the effects of climate warming on seasonal growth pattern of sapling Qinghai spruce, and (2) the influence of climate warming on stem growth.

2. Materials and methods

2.1. Study area and tree species

This study was conducted in a Qinghai spruce stand with trees ranging in age from 20 to 60 years. The stand was located on a north-facing slope at 2700 m elevation in the Pailugou watershed in the central Qilian Mountains of China (100°17′05″E, 38°33′19″N). The main soil type is gray-cinnamon soil with a calcareous rock parent material, coarse texture, and average soil depth of 1.2 m. Soil surface is covered with a about 10-cm thick layer of moss. The area has a continental climate with cold winters and warm summers. Measured since 2001, mean annual air temperature was 0.5 °C, and mean annual maximum and minimum air temperatures were 28.0 and -36.0 °C, respectively. The mean annual precipitation was 375.5 mm, of which 70% fell from May to September. Qinghai spruce is the only evergreen arbor and it is also the dominant tree species at the study site.

An open-top chamber (OTC) made of plastic was set up in the forest stand to increase air temperature for our study. The OTC was 2.5 m high, and 5 × 5 m^2 (Fig. 1). One control plot was established outside the chamber (OC). Based on a survey of diameters at breast height of all the sapling trees at the study site, four Qinghai spruce trees of average diameter were selected (Table 1). The first two trees were growing within the OTC, and the others in the OC.

2.2. Dendrometer records and related parameters

During the growing seasons of 2014–2016, high-resolution automatic point dendrometers (EcoMatik, Germany; type DR, accuracy ± 2 μm, temperature coefficient < 0.1 μm/K) were employed to measure stem radial changes in Qinghai spruce. Dendrometers were installed on four trees at a height of 0.5 m. To reduce the effects of bark expansion and shrinkage on the accuracy of measurement, parts of the bark were carefully removed without damaging the cambial zone. Changes in stem radial growth, representing a combination of reversible shrinkage and expansion, and irreversible radial growth, were recorded continuously every 30 min using a data logger (EcoMatik, Germany). Stem radial increment (SRI) and tree water deficit (TWD), reflecting daily stem radial growth and drought stress of trees, respectively, were extracted from the dendrometer measurements data.

As a physiological measure of drought stress (Zweifel et al., 2005;

Table 1
Characteristics of the study trees.

Trees	Diameter at breast height(cm)	Height(m)	Age(year)	Site
Tree1	7.6	3.5	37	OTC
Tree2	6.9	3.3	34	OTC
Tree3	6.7	3.0	35	OC
Tree4	6.4	2.8	30	OC

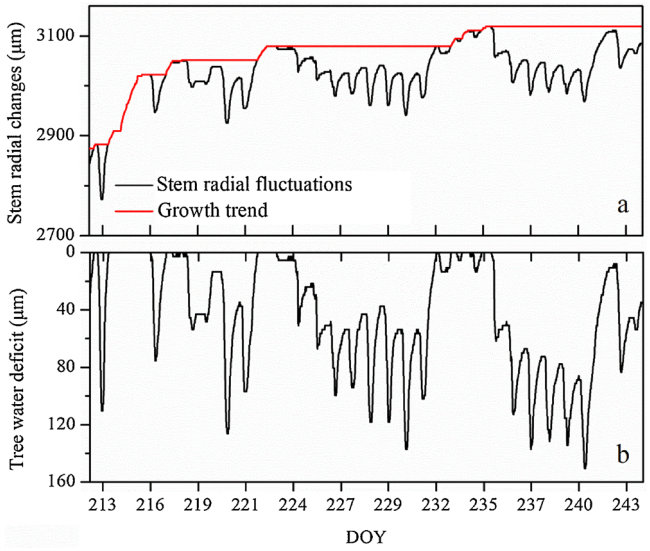

Fig. 2. Example of tree water deficit calculation, showing the stem radial fluctuations (black line) and the growth trend according to the zero growth concept (red line) (a), tree water deficit, as the difference between the growth trend and stem radial fluctuations (b). a and b are examples of data recorded in Tree 2 between DOY 213–243 of 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Drew et al., 2011), TWD can be determined using the zero-growth concept as described in Zweifel (2016) (Fig. 2a, b). TWD was calculated as the difference between the past highest stem radial record (SRmax) and current stem radial reading (SRt) when SRt < SRmax, with TWD = 0 when SRt exceeded SRmax (Zweifel et al., 2016) (Fig. 2a, b). A TWD of zero indicated the optimal water content of the cambial zone, while increasingly positive values meant increasing water stress. For the purpose of this paper, the 30-min TWD data for each tree were transformed to daily-averaged values (Fig. 3a–c). Then, based on the two trees for each group (OTC and OC), mean TWD and averaged 10-day interval TWD were calculated for further analysis.

The stem cycle approach can be divided into three distinct phases over approximately 24 h (Downes et al., 1999): (a) contraction phase, (b) recovery phase, and (c) stem radial increment phase. Based on the circadian cycle, SRI was obtained from each tree by calculating the difference between daily maximum stem radial changes over two days (Fig. 3d–f). Then, based on the two trees in each treatment (OTC and OC), mean SRI and averaged 10-day interval SRI were calculated for further analysis.

2.3. Estimation of the main growing season

To study the effects of an increase in temperature on Qinghai spruce, it is needed to clear the main growing season. The Gompertz function is one of the most effective models to describe growth patterns. It has been widely used to model tree growth patterns due to its practicability and asymmetrical shape (Rossi et al., 2003; Duchesne et al., 2012). We employed the model to explore the growth pattern of Qinghai spruce from late April to late September of 2014–2016. The model was fitted to the daily averaged raw measurement data, and the function was as follows:

$$Y = Y_0 + A\exp[-e^{(\beta - \kappa t)}] \quad (1)$$

where Y was the daily averaged raw measurement, Y_0 and A were the lower and upper asymptotes, respectively, β and κ were the x-axis placement parameter and the rate of change parameter, respectively, and t was time in days. Ordinary least squares method was employed for parameter estimation (Duchesne et al., 2012; Wang et al., 2014). Then, we calculated the first derivative to obtain the daily growth rates, modeling the daily growth increment. To assess the artificial warming

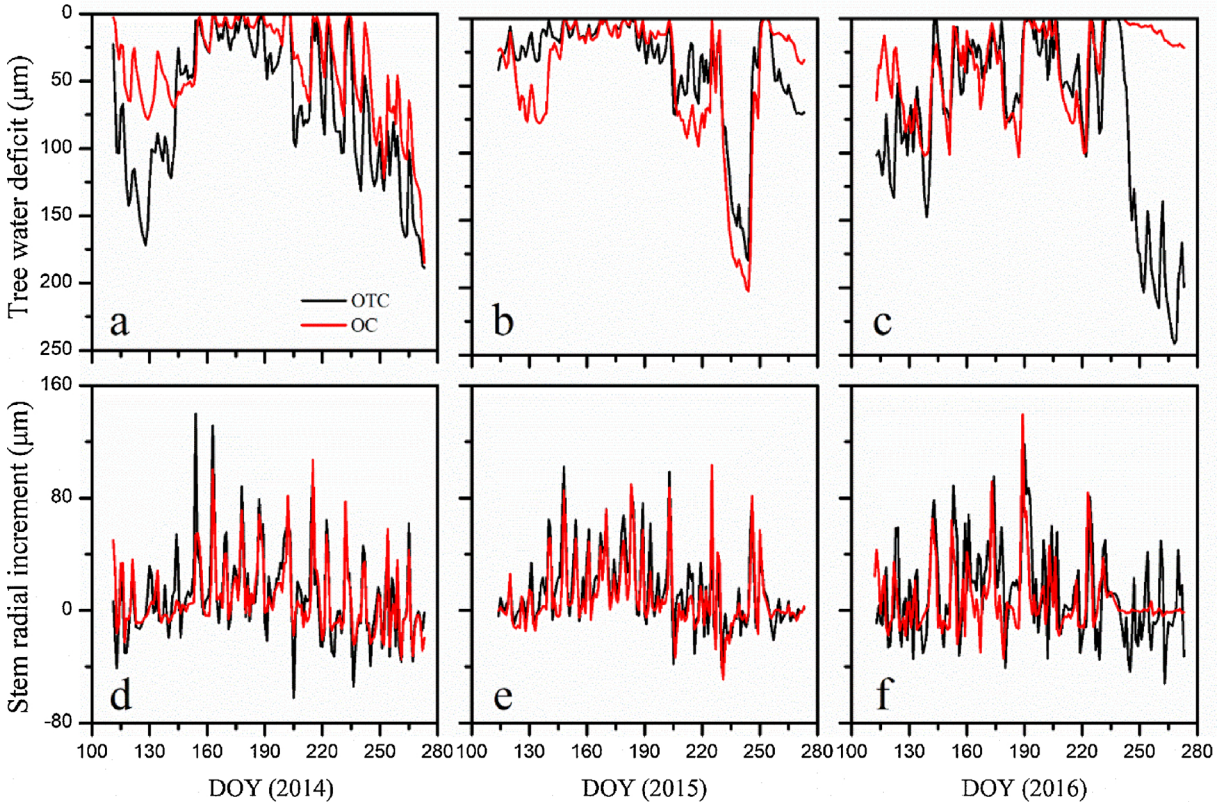

Fig. 3. Averaged tree water deficit (a, b, c) and stem radial increment (d, e, f) for each treatment during the growing seasons of 2014–2016.

effect, daily averaged stem radial changes of two trees in the two groups (OTC and OC) for each year were modeled (Fig. 6). Taking into account the accuracy of dendrometer (± 2 μm) and the changes in daily growth rates in different periods, we defined the main growth period as all days when daily growth rates > 4 μm/day.

2.4. Environmental data

To access the relationships between stem radial increment and tree water deficit and environmental factors, a weather station was installed in the study site during the seasonal growth period of 2014–2016. Further, another temperature and humidity sensor from the weather station was installed in the OTC. Precipitation (P, mm), air temperature and relative air humidity in the OTC and the OC (T-OTC, T-OC, °C; RH-OTC, RH-OC, %) were recorded. The vapor pressure deficit between the two treatments (VPD-OTC, VPD-OC, kPa) was calculated from the values of air temperature and relative air humidity. Two 5 T M sensors (Decagon Devices Inc., Pullman, WA, USA) were installed near the monitored trees in the OTC and the OC, respectively, to continuously measure soil water content (SWC-OTC, SWC-OC, m^3 m^{-3}) and soil temperature (Tsoil-OTC, Tsoil-OC, °C). Em50 data loggers were employed to collect data. Soil water content and temperature were measured at 40 cm depth due to root distribution up to 40 cm. All the environmental factors were recorded every 30 min synchronously with the dendrometer measurements, and were later averaged per day (Fig. 4).

2.5. Data analysis

To evaluate the warming effect of the open-top chamber, differences in air and soil temperatures, relative air humidity, vapor pressure deficit, and soil water content between the OTC and OC were calculated using the paired-sample *t*-test (Fig. 5). Differences in stem radial changes (SRI and TWD) between the two treatments were also tested during the monitoring periods (Table 3). Pearson correlation analysis was used to analyze the relationships between stem radial changes and environmental factors (T, RH, VPD, SWC and Tsoil). Due to the abnormal distribution of precipitation data, nonparametric Spearman correlation coefficients were calculated to quantify the relationships between SRI and TWD and P (Fig. 7). In addition, the negative values of SRI were replaced by zero in the correlation analysis. All the analyses were carried out in SPSS 17.0 software (SPSS Inc. Chicago, USA).

3. Results

3.1. Environmental variables

During the monitoring periods (from late April to late September) of 2014–2016, average air temperatures were 9.9 ± 4.4, 10.2 ± 4.2 and 11.3 ± 4.7 °C in OC, and 10.9 ± 4.3, 11.2 ± 4.2 and 12.2 ± 4.7 °C in OTC, respectively for 2014, 2015, and 2016 (Fig. 4a–c). Maximum air temperatures were recorded in late July and early August. Total amount of precipitation for the monitoring periods was 403.2, 389.5, and 387.2 mm, respectively for 2014, 2015, and 2016, accounting for more than 85% of the annual total precipitation each year. Relative air humidity and vapor pressure deficit ranged from 8.4–99.4 %, and from 0 to 1.49 kPa (Fig. 4d–f), respectively. Soil temperature varied with air temperature and ranged from -1.0 to 10.8 °C depending on treatment. Soil temperatures in OTC were higher than those in OC at the beginning of monitoring periods, and then reversed (Fig. 4g–i). Average soil water

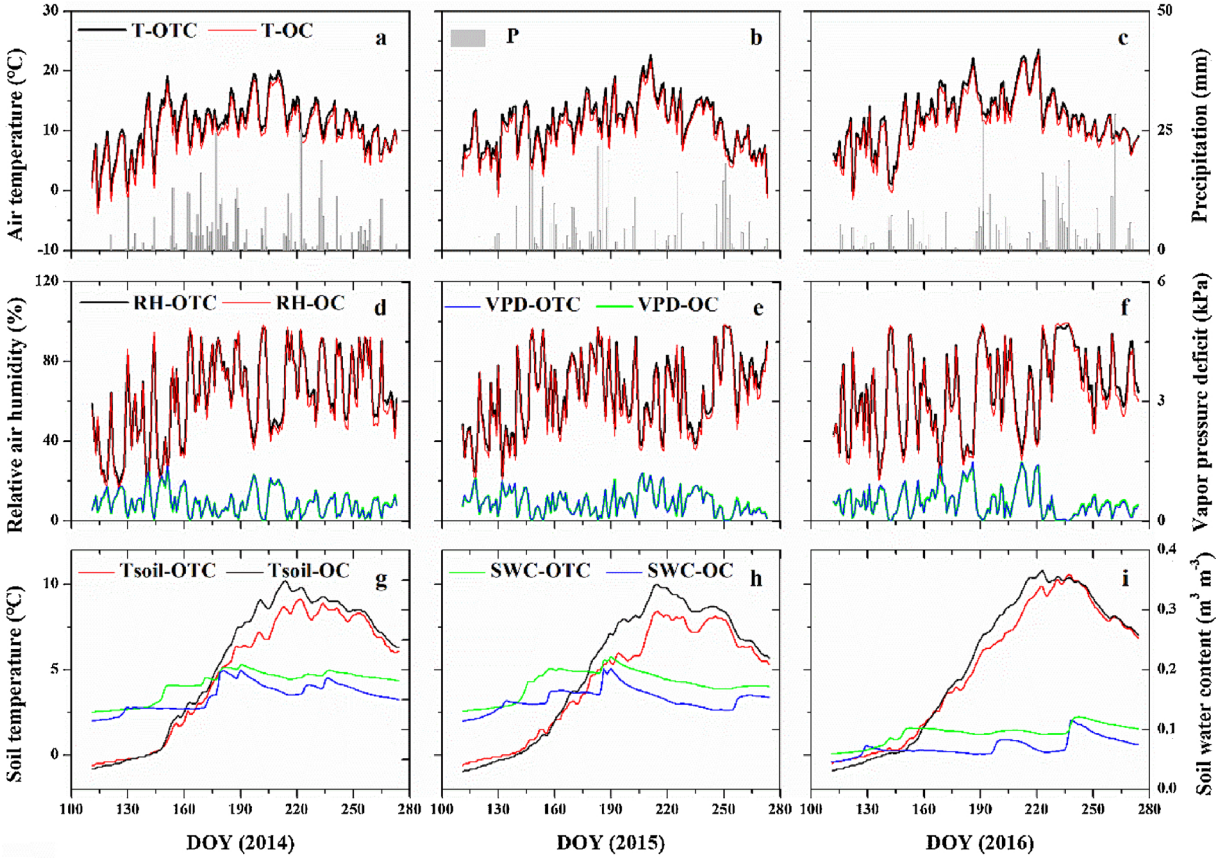

Fig. 4. Time series of air temperature (T-OTC, T-OC) and precipitation (P) (a, b, c), relative air humidity (RH-OTC, RH-OC) and vapor pressure deficit (VPD-OTC, VPD-OC) (d, e, f), soil temperature (Tsoil-OTC, Tsoil-OC) and soil water content (SWC-OTC, SWC-OC) (g, h, i) in the open-top chamber (OTC) and out of the chamber (OC) during the growing seasons of 2014–2016.

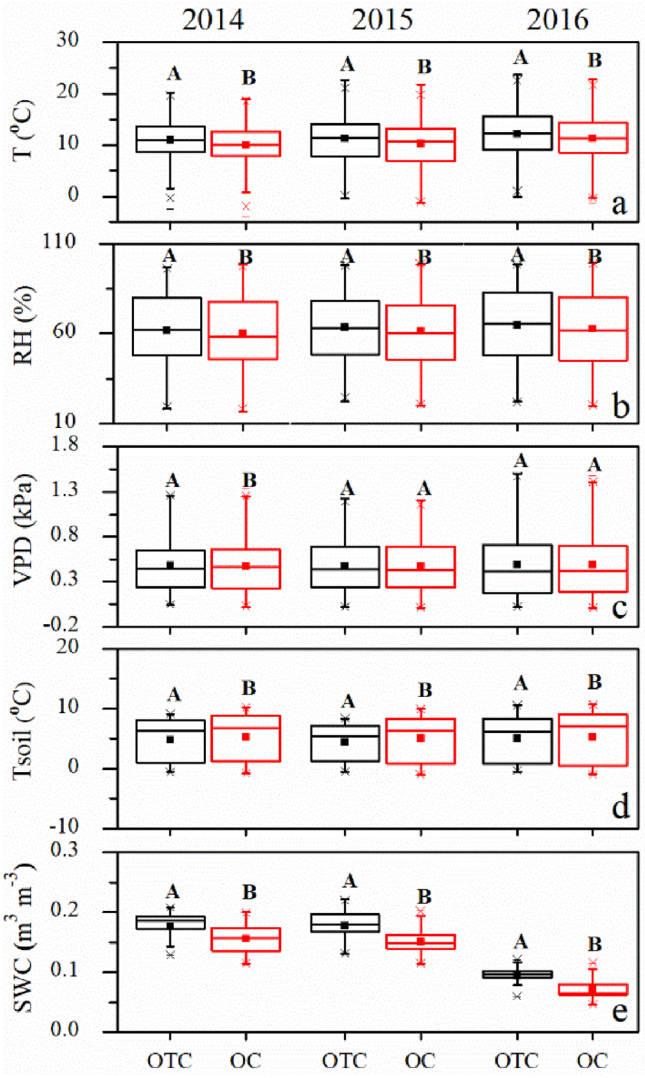

Fig. 5. T, RH, VPD, Tsoil and SWC (a–e) in the open-top chamber (OTC) and out of the chamber (OC) during the growing seasons of 2014–2016. Box plots description: the length of the box represents the interquartile range (25th–75th percentile), the dot inside the box represents the mean, the horizontal line in the box interior represents the median, vertical lines extend to the minimum and maximum values, and outliers are marked with an asterisk. Different capital letters represent statistically significant differences between the two treatments ($p < 0.01$).

contents were 0.176 ± 0.024, 0.177 ± 0.024, and 0.094 ± 0.016 $m^3 m^{-3}$ in OTC, and 0.156 ± 0.024, 0.151 ± 0.018, and 0.071 ± 0.015 $m^3 m^{-3}$ in OC, respectively for 2014, 2015, and 2016. Paired-sample *t*-tests showed that there were significant differences in air temperatures between OTC and OC (Fig. 5a), with difference values of 1.02 ± 0.35, 0.98 ± 0.38, and 0.86 ± 0.37 °C, respectively for 2014, 2015, and 2016. Relative air humidity also exhibited a significant difference between the two conditions (Fig. 5b), with difference values of 1.64 ± 1.87, 2.28 ± 1.77, and 2.17 ± 2.07%, for the respective years. Vapor pressure deficit, however, was significantly different only in 2014, with a difference value of 0.006 ± 0.027 kPa (Fig. 5c). Soil temperature in OC was higher than in OTC, and the difference values were 0.56 ± 0.56, 0.66 ± 0.81 and 0.27 ± 0.59 °C (Fig. 5d), respectively for 2014, 2015, and 2016. However, soil water content in OTC was higher than in OC, and the difference values were 0.02 ± 0.01, 0.03 ± 0.01, and 0.02 ± 0.01 $m^3 m^{-3}$ (Fig. 5e), respectively for the three years of study.

3.2. Seasonal growth patterns

Average stem radial changes in the treatment and in the control trees were modeled (Fig. 6a–c). Nonlinear regressions explained > 98% of the variability in dendrometer measurement data. During the study, the onset of the main growth period in the OTC was significantly earlier than in the OC (Fig. 6, Table 2). The cessation of the main growth period did not exhibit a significant difference between the two conditions. The length of the main growth period ranged from 87 days to 107 days in the OC, and from 95 days to 110 days in the OTC.

3.3. The response of SRI and TWD to environmental factors

Pearson and Spearman correlation coefficients were calculated to quantify the relationships between environmental factors and SRI and TWD in Qinghai spruce (Fig. 7). SRI exhibited significant negative correlations with T ($r = -0.321$, $p < 0.01$; $r = -0.436$; $p < 0.01$) and VPD ($r = -0.528$, $p < 0.01$; $r = -0.571$; $p < 0.01$) in the OTC and OC. Meanwhile, SRI was positively correlated with RH ($r = 0.599$, $p < 0.01$; $r = 0.616$; $p < 0.01$) and precipitation ($\rho = 0.596$, $p < 0.01$; $\rho = 0.595$; $p < 0.01$) in both conditions. SWC and Tsoil were not significantly correlated with SRI. TWD were positively correlated with T ($r = 0.335$, $p < 0.01$; $r = 0.468$; $p < 0.01$) and VPD ($r = 0.586$, $p < 0.01$; $r = 0.627$; $p < 0.01$), and negatively correlated with RH ($r = -0.607$, $p < 0.01$; $r = -0.586$; $p < 0.01$), precipitation ($\rho = -0.604$, $p < 0.01$; $\rho = -0.544$; $p < 0.01$), and SWC ($r = -0.193$, $p < 0.01$; $r = -0.274$; $p < 0.01$) in both conditions. Tsoil was not significantly correlated with TWD.

3.4. Stem radial changes

The cumulative seasonal growth was 1.72, 2.17, and 2.10 mm in OTC, and 1.35, 1.33, and 1.05 mm, in OC respectively in 2014, 2015, and 2016 (Table 2). Mean growth rates were 18.08 ± 9.41 μm/d in 2014, 19.73 ± 10.87 μm/d in 2015, and 19.85 ± 11.02 μm/d in 2016 in OTC, and 15.57 ± 7.59, 15.24 ± 7.44, and 9.79 ± 3.34 μm/d, in the corresponding study years in OC. During the main growth period, the cumulative seasonal growth and mean growth rates in OTC were greater than those in OC.

The paired-sample *t*-test showed that there was a significant difference in SRI between the two growth conditions in 2015 (5.09 ± 5.17 μm), and a significant difference in TWD in 2014 (28.42 ± 23.80 μm) and 2016 (39.78 ± 72.28 μm) during late April to late September (Table 3); additionally, significant differences in SRI were observed in 2014–2016 during the middle of May to early August, and in TWD in 2014 (Table 3). SRI in OTC was significantly higher than in OC, while TWD was not significantly different between the two treatments from the middle of May to early August in the three years of study (Fig. 8).

4. Discussion

4.1. The effect of artificial warming on seasonal growth pattern

In our study, the initiation of the main growth period ranged from DOY 127 in 2015 in OTC to DOY 145 in 2014 in OC (Table 2). Previous studies have shown that air temperature was one of the most important factors controlling the onset of cambial activity and cell production by influencing the rate of cell division and the amount of xylem produced (Deslauriers and Morin, 2005; Deslauriers et al., 2008; Moser et al., 2010; Rossi et al., 2011; Lenz et al., 2013). However, we found that the beginning of the main growth period in Qinghai spruce was related to soil temperature rather than air temperature, and started when soil temperature reached around 0 °C at the depth of 40 cm (Table 4). Therefore, at the beginning of monitoring periods, high soil temperature in the OTC resulted in earlier about a week of onset of main growth

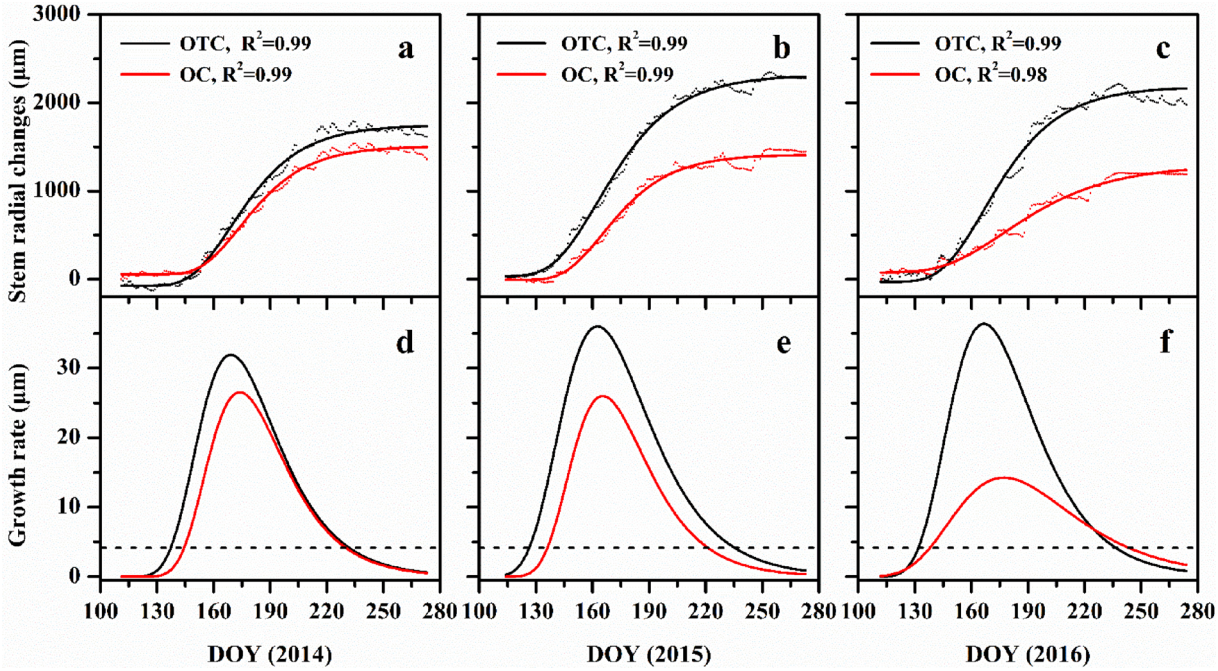

Fig. 6. Observed and modeled stem radial changes. Daily average measurements (dots) and Gompertz-function modeled curves (lines) (a, b, c), and modeled daily growth rates (d, e, f). Dashed lines in the bottom panels represent daily growth rates equal to 4 μm/day. OTC and OC mean the open-top chamber and out of the chamber, respectively.

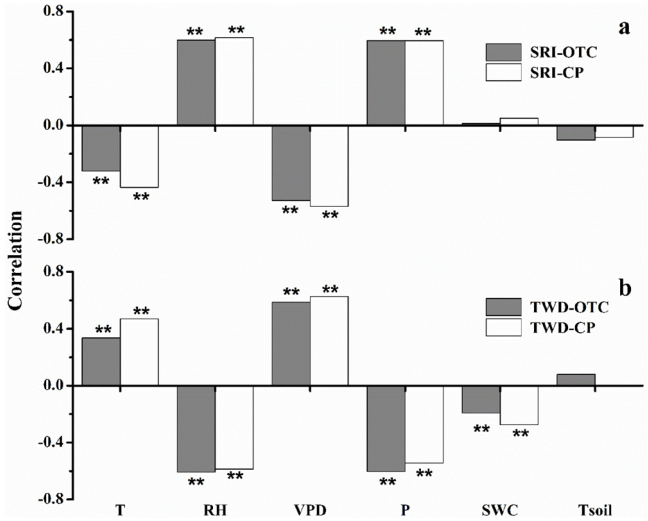

Fig. 7. Correlation coefficients between stem radial increment (SRI) and tree water deficit (TWD) and main environmental factors. T: daily mean air temperature; RH: relative air humidity; VPD: vapor pressure deficit; P: precipitation; SWC: soil water content; Tsoil: soil temperature. **represents significance level at $p < 0.01$.

Table 3
Paired-sample *t*-test (mean, standard deviation (SD), and p-value) for SRI and TWD in the OTC and OC conditions for late April (L-Apr) to late September (L-Sep), and for mid-May (M-May) to early August (E-Aug) for three years of study.

		SRI $_{OTC-OC}$			TWD $_{OTC-OC}$		
		2014	2015	2016	2014	2015	2016
From L-Apr to L-Sep	Mean	1.27	5.09	4.71	28.42	−7.47	39.78
	SD	7.14	5.17	11.2	23.8	23.28	72.28
	p-value	0.487	0.001	0.113	0.001	0.219	0.044
From M-May to E-Aug	Mean	4.25	8.73	11.89	15.37	−9.65	−3.55
	SD	5.28	2.94	8.54	17.09	20.66	11.2
	p-value	0.042	0.001	0.003	0.027	0.199	0.370

OTC − OC: values of the difference between the inside and the outside of the chamber.

period compared with the growth in OC. When soil temperatures reach above 0 °C, frozen soil melts, and water becomes available to roots. At the same time, warmer soils facilitate root water uptake when growth begins. Our results indicated that an increase in soil temperature before the beginning of growth advanced the initiation of the main growth period, which was consistent with other studies (Tardif et al., 2001; Gruber et al., 2009). However, soil temperature is affected by air temperature which affected by climate changes; therefore, the

Table 2
Characterization of seasonal growth patterns in years 2014–2016.

Year	Tree condition	Timing of growth initiation (DOY)	Timing of growth cessation (DOY)	Length of growing season (days)	Cumulative seasonal growth (mm)	Mean growth rate (μm/d)
2014	**OTC**	138	232	95	1.72	18.08 ± 9.41
	OC	145	231	87	1.35	15.57 ± 7.59
2015	**OTC**	127	236	110	2.17	19.73 ± 10.87
	OC	136	222	87	1.33	15.24 ± 7.44
2016	**OTC**	132	237	106	2.10	19.85 ± 11.02
	OC	138	244	107	1.05	9.79 ± 3.34

OTC: in the open-top chamber; OC: out of the chamber.

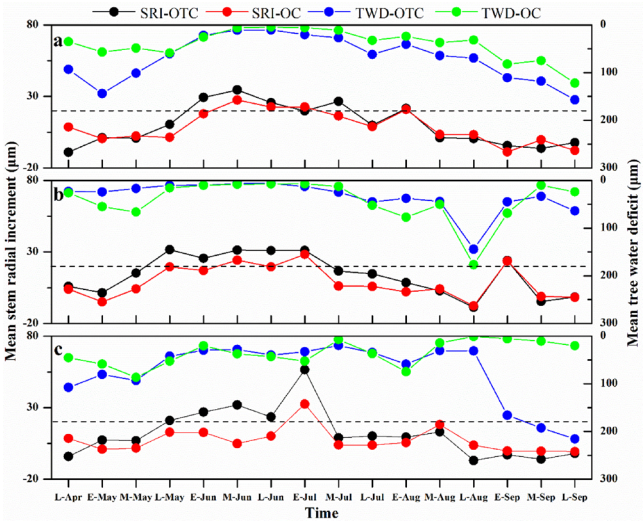

Fig. 8. Ten-day mean stem radial increment (SRI-OTC, SRI- OC) and tree water deficit (TWD-OTC, TWD-OC) in 2014 (a), 2015 (b), and 2016 (c). Dashed lines in panels b and c represent mean stem radial increment of 0 μm. OTC and OC represent open-top chamber and out of the chamber, respectively.

Table 4
Characterization of air and soil temperature (°C) ten days before the beginning of growth.

		2014		2015		2016	
		OTC	OC	OTC	OC	OTC	OC
Tmax	Mean	20.00	16.83	17.14	15.49	19.46	11.72
	SD	6.35	5.08	4.80	4.75	5.58	5.58
Tmean	Mean	8.67	9.94	6.02	9.10	7.93	5.99
	SD	4.34	4.42	2.32	4.42	3.22	4.13
Tmin	Mean	1.37	3.21	−0.33	3.48	0.46	0.64
	SD	3.13	3.51	2.33	4.33	3.11	3.60
Tsoil	Mean	−0.07	0.26	−0.14	−0.13	0.06	−0.02
	SD	0.11	0.26	0.07	0.14	0.11	0.11

OTC: open-top chamber; OC: out of the chamber; Tmax: maximum air temperature; Tmean: mean air temperature; Tmin: minimum air temperature; Tsoil: soil temperature.

beginning of the main growth period may be expected to advance with climate warming.

In our study, the timing of cessation of the main growth period ranged from DOY 222 in 2015 to DOY 244 in 2016 in OC (Table 2). Variability in the timing of cessation was much higher than in the timing of the onset of the growth period, suggesting that air or soil temperature may not have been the main factor affecting growth cessation (Table 5) (Moser et al., 2010; Wang et al., 2014). Other studies reported that summer water deficit affected the timing of growth cessation (Levanič et al., 2008; Oberhuber et al., 2014). However, during growth cessation in our study, precipitation was sufficient to supply moisture to trees (Table 5), indicating that summer water deficit had little influence on determining growth cessation in Qinghai spruce (Moser et al., 2010). Several studies suggested that cessation of the main growth period was related to internal physiological mechanisms rather than environmental factors. Oberhuber et al. (2014) showed that root distribution and water use efficiency played a vital role in influencing the end of growth. Moser et al. (2010) reported that growth cessation was controlled by photoperiod. Duchesne e al. (2012) showed that the end of the growing season depended on the number of xylem cells produced.

Table 5
Characterization of air and soil temperature, and precipitation ten days before the end of growth.

		2014		2015		2016	
		OTC	OC	OTC	OC	OTC	OC
Tmax	Mean	23.69	16.51	24.90	21.63	20.37	14.62
	SD	5.37	2.78	4.28	3.31	4.59	1.73
Tmean	Mean	11.95	11.01	11.95	15.70	14.58	11.51
	SD	2.60	2.52	2.69	3.09	1.80	1.62
Tmin	Mean	6.35	6.61	5.31	10.72	11.18	8.81
	SD	1.79	1.96	2.20	2.36	1.22	2.38
Tsoil	Mean	8.39	9.34	7.60	9.82	10.07	10.23
	SD	0.42	0.37	0.39	0.11	0.28	0.12
P	Sum	32.4	31.3	7.7	10.7	62.9	48.0

OTC: open-top chamber; OC: out of the chamber; Tmax: maximum air temperature; Tmean: mean air temperature; Tmin: minimum air temperature; Tsoil: soil temperature; P: precipitation.

4.2. Environmental control on SRI and TWD

SRI reflects the daily stem radial growth, and TWD is an indicator of tree drought stress, and both are complex physiological responses to environmental variability. In our study, environmental factors affected SRI and TWD in a similar manner in OTC and OC during the main growth periods (Fig. 7).

T and VPD had significant negative effects on SRI, indicating moisture stress. In the soil-plant-atmosphere continuum, moisture moves along a gradient from a higher soil water potential to a lower atmospheric water potential. Previous studies reported that high temperature and VPD may decrease atmospheric water potential, influence the rate of transpiration, and promote closure of stomata, decreasing carbon uptake and photosynthetic efficiency, and limiting growth (Zweifel et al., 2006; Vieira et al., 2013). However, respiration rates increased under high temperature conditions as a result of accumulation of carbohydrates (Jiang et al., 2015). The significant positive response of SRI to RH and precipitation in our study indicated moisture recharge. Precipitation and high RH decrease the rate of transpiration and indirectly increase cell turgor, driving cell division and irreversible expansion of the existing cells (Zweifel et al., 2006; Kocher et al., 2012). On the other hand, precipitation recharges soil water, increasing soil water potential and directly alleviating water shortage in trees. SRI was not significantly correlated with SWC and Tsoil in this study, which was likely due to higher soil water content and a smaller range of changes throughout the main growth period (Devine and Harrington, 2009, 2011).

Several studies reported that TWD was positively correlated with T and VPD (Zweifel et al., 2005; Drew et al., 2011; Oberhuber et al., 2015a, b), and that was consistent with our results. This indicated that drought stress intensified with high temperature and vapor pressure deficit. High values of both factors decrease atmospheric water potential, and increase sap flow and water loss by transpiration, increasing drought stress (Sánchez-Costa et al., 2015; Li et al., 2016). TWD was significantly negatively related with RH, precipitation, and SWC in this study, and this can be explained by water supply to root and tree transpiration. Precipitation recharged soil water and increased relative air humidity, decreasing tree water deficit by increasing root moisture and reducing tree transpiration. Meanwhile, due to the lower VPD and higher RH on overcast or rainy days, transpiration rate may be lower, resulting in a decrease in tree water stress (Devine and Harrington, 2011; King et al., 2012). SWC was not significantly correlated with SRI, but was negatively correlated with TWD. These results may indicate that, on sunny days, most of the soil water was used for transpiration, and only some water was applied to tree growth.

4.3. Effects of warming on stem radial changes

Several authors have reported that cumulative tree growth was associated with duration of the growing season (Takahashi, 2010; Wang et al., 2014). In our study, cumulative tree growth did not increase with the length of the growing season (Table 2). Cumulative seasonal growth in OTC was higher than in OC, possibly indicating that high temperature promoted the growth of sapling Qinghai spruce. However, the largest cumulative seasonal growth appeared in 2015 in OTC, and in 2014 in OC, while the highest average temperature was recorded in 2016. These results indicated that cumulative seasonal growth may be influenced by complex environmental factors. Paired-sample *t*-test for SRI and TWD between the two conditions suggested that a warming effect mainly influenced stem radial growth during the main growth period (Table 3), and the impact on TWD was not significant.

5. Conclusions

In this study, we assessed the response of stem radial changes in four young Qinghai spruce trees to environmental variables over three growing seasons in the field and in an open-top chamber. We concluded that higher soil temperatures resulted in an advance in the initiation of the main growth period, while the end of growth was not related to environmental variables. Stem radial growth and tree water stress were affected by a combination of air temperature, relative air humidity, vapor pressure deficit, precipitation and soil water content. Cumulative seasonal growth may be influenced by air temperature, and by interacting environmental factors. The effect of climate warming on stem radial increment may be larger than that of tree water deficit.

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